SOME MORPHOLOGICAL PECULIARITIES OF THE NYMPHAEACEAE AND HELOBIAE.*

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Having spent some time in studies upon various species belonging to the Helobiae, the writer has naturally taken considerable interest in the recent investigations by Lyon, Cook and others on the embryogeny of the Nymphaeaceae. On account of certain peculiarities in the anatomical structure of these plants, the writer following many others had reservedly placed the Nymphaeaceae near the Helobiae; but, because of the supposed characteristic Dicotyl embryo and certain Dicotyl features which were read into the flowers, it was thought improper to take them away from their "authoritative" position. However, since the way has been considerably cleared by Lyon and Cook, at least so far as the embryo is concerned, for judging certain other characters of the group on their merits, a considerable study has been carried on for the last three years upon various species of the group.

It might perhaps be proper to state here that the writer had the pleasure of examining most of Cook's preparations on which his more important conclusions were based; even going so far as to reconstruct the early stages of the embryo which showed that in Nymphaea advena the development of the so-called cotyledon is essentially the same as what Lyon had reported for Nelumbo. It is unfortunate that Coulter and Chamberlain in their "Morphology of Angiosperms" overlooked the reference to Cook's embryo of Nymphaea advena. For the fact that the embryo of Nymphaea has such a close resemblance to Nelumbo must have a very important bearing on the subject.

As is well known, the vascular bundles of the Nymphaeaceae are essentially Monocotyl in type, showing the characteristic closed bundle. So striking is this in the bundles of the flower stem of Nelumbo that one might almost palm off a section for a corn bundle. The disposition of the xylem and vessels, the phloem, and the cap of sclerenchyma, taken together with the scattered arrangement and the absence of secondary cambium certainly represent a structure characteristic of Monocotyls (Fig. 1). The vascular bundles of Podophyllum and certain species of Piperaceae which the writer examined are considerably different and show the open type of bundle characteristic of Dicotyls. These plants have therefore no important bearing on the relationship of the Nymphaeaceae so far as the anatomy of the stem is concerned.

The many superficial characters must also be taken into consideration. The similarity of habitat, the rhizome habit, the

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striking agreement of some of the leaf forms, and the general character of the flowers at once suggest the Helobiae as near relatives; and though such characters could not be of first rank in making a final disposition of the group, they do not in the least stand in the way but rather assist in disposing of the water lilies as Monocotyls.

Since there has been a strong tendency to read Dicotyl characters into the flowers of some water lilies, the writer took the opportunity to make a study of the flower of a few representative species of Naiadales and Nymphaeaceae in order to see how well the floral plan could be made to fit into the Monocotyl scheme. It is certainly much easier to read Monocotyl characters into the flowers than Dicotyl. The mere position in which a species is placed may have much to do with its description. For instance, the perianth of Nymphaea advena is described as having six sepals and an indefinite number of stamen-like petals. These staminodes, the so-called "petals," are so evidently only very slightly modified stamens that in many cases a superficial examination will not distinguish them. The perianth is then typically trimerous with three sepals aud three petals. This is of course of no special importance, for many of the true Ranales also have a trimerous perianth.

In Castalia the sepals are said to be four and the petals numerous. This is sometimes the case; but in Castalia odorata (Fig. 11) the sepals are normally three in a cycle, but sometimes by the expansion of the receptacle one of the segments of the second cycle is partly or nearly completely brought to the outside. Its relationship to the inner cycle is, however, always evident. The second cycle of three segments usually with some green on the outside, must therefore be regarded as corresponding to the second cycle in Cabomba or Nymphaea and all the rest of the petal-like segments may be staminodes. In Castalia tuberosa (Fig. 12) the dispacement by expansion is normal and there are four green segments, but the one "sepal" still clearly shows its relation to the inner cycle. This tendency of the floral organs to fall into sets of four is very prominent in some Helobiae as in the various species of Potamogeton (Fig. 9).

The transition from comparatively simple flowers to those with great numbers of parts as appears in passing from Cabomba to Nymphaea is also characteristic of the Alismaceae. The extreme numbers no doubt represent multiplication or augmentation. In Alisma the parts are few (Fig. 2), in Sagittaria rigida (Figs. 3, 4) the numbers are greater, but still small when compared with the carpellate flowers of Sagittaria latifolia, where the carpels count up to sixteen hundred, more or less (Figs. 5, 6). Staminodes are also a prominent character in various Helobiae as in Sagittaria rigida, Vallisneria, Philotria, Butomus, and Limnocharis.

Although there is much variation in the number of parts, typical specimens were selected to represent the diagrams accompanying this paper. Each diagram given represents an actual flower of the species. The descriptions following represent what to the writer appears to be the correct characterization, so far as number and arrangement of parts are concerned, of the flowers of the species studied:

Cabomba caroliniana Gr.—Flowers hypogynous, pentacyclic, actinomorphic, trimerous, with all the parts separate; sepals 3, petals 3, stamens 6, carpels 3 more or less (Fig. 7).

Brasenia purpurea (Mx.) Casp.—Flowers hypogynous with all the parts separate; perianth cyclic, trimerous; androecium and gynoecium spiral, stamens 18 more or less, carpels 9 more or less (usually 6–18) (Fig. 8).

Nymphaea advena Sol.—Flowers hypogynous with the parts separate except in the gynoecium; calyx and corolla cyclic, trimerous; androecium and staminodes spiral; staminodes stamen-like, 18 more or less; stamens 250 more or less, arranged in spirals with about 14 circles of 18 stamens each; gynoecium cyclic of 18 carpels more or less, completely united in 1 cycle forming a plurilocular ovulary (Fig. 10).

Castalia odorata (Dry.) W. & W.—Flowers with partly epigynous stamens, staminodes and perianth; calyx cyclic of 3 sepals; corolla and staminodes not separable, spiral; original petals probably 3, the staminodes arranged in about 7 circles of 6 divisions each, passing gradually into fertile stamens; stamens 100 more or less, spirally arranged in about 17 circles of 6 divisions each; carpels 18 more or less, united in 1 cycle forming a plurilocular ovulary (Fig. 11).

Castalia tuberosa (Paine) Greene.—Flowers with numerical plan about the same as in C. odorata, but the arrangement much displaced so that there are apparently 4 sepals, and 4 petals of the second cycle. There is also a disarrangement of the staminodes (Fig. 12).

Nelumbo lutea (Willd.) Pers.—Flowers hypogynous with 2 dimerous cycles of sepals and 3 petals in the first corolla cycle; the remaining petals or highly modified staminodes spirally arranged in about 7 circles of 3 each; stamens 150 more or less, spirally arranged, falling into 6 circles of 24 each; carpels 18 more or less, distinct, situated in pit-like depressions of the large top-shaped receptacle, arranged into several imperfect circles of 3s, 6s, 9s, etc., representing a primitive spiral arrangement (Fig. 13).

There has been no constancy in the progressive development of the ovule in the Helobiae; for in the epigynous Hydrocharitales we have both orthotropous and anatropous ovules, while in the hypogynous Alismaceae as in Alisma and Sagittaria the ovule

passes in its development from orthotropous, through the anatropous condition and becomes campylotropous when mature. The setting aside of the lower endosperm nucleus of the first division by a wall and its development as a large vesicular cell, as is the case in Sagittaria and Vallisneria, while not confined to the Helobiae nor apparently characteristic of all of them, is yet significant when one finds a similar peculiarity in some of the Nymphaeaceae.

The number of ovules in the carpel also shows a diverse development. In Potamogeton, Alisma, Sagittaria and Nelumbo there is usually a single ovule in each ovulary. In Butomus, Vallisneria and other genera of the Hydrocharitales the ovules are scattered on the inner surface of the ovularies. This is also one of the striking characters of Nymphaea and Castalia. In fact the peculiar way in which the ovularies of certain Nymphaeaceae agree with many of the Hydrocharitales must appear most interesting to anyone who has made the comparison. Coalescence and epigyny also figure in both the Hydrocharitales and Nymphaeaceae. Thus it will appear that what might be considered as minor or secondary characters do not detract but rather add considerably to the weight of the argument that the Nymphaeaceae have very much in common with the Helobiae.

The important investigation of Lyon shows conclusively that he was correct in claiming that the embryo of Nelumbo is essentially of the "Monocotyl" type, and, since there can be no question of the facts, it also appears that his further conclusion was unavoidable that the Nymphaeaceae should be placed near the Helobiae. As stated before, the writer had the opportunity of studying some of Cook's preparations and it became evident that the embryo of Nymphaea advena is in all essentials similar to that of Nelumbo. Later a special study was made of the young embryo of Nymphaea advena. As stated by Cook, in the young embryo of Nymphaea the "cotyledon" is at first not lobed. Later there is a rapid development at the two sides resulting in a two-lobed structure (Figs. 14, 15). Since Conrad stated that in Castalia odorata the embryo has two distinct "cotyledons" from the first, a study was also made of this species. With some difficulty very young embryos were dissected out of their embryosacs which are easily removed from the ovule. It was found that although the "Dicotyl" appearance is quite strong, the embryo must be regarded as of the same type as Nymphaea and Nelumbo. In the very young embryo there is an expansion which extends nearly around the base but is discontinuous at one side (Fig. 16). Soon this expansion develops on opposite sides as two prominent lobes in such a manner that the original connection between the two lobes is very difficult to distinguish (Fig. 17). On examining the embryo from below, however, the similarity to the Nelumbo and Nymphaea embryos becomes perfectly apparent (Figs. 18,

19). There is the same opening on one side, and on the back a connection of the two lobes, only to a less extent. Unless special care were taken in reconstructing such an embryo from serial sections, one might readily take it for a Dicotyl. It will be evident, however, from a comparison of the figures that the Castalia embryo represents only the extreme of the lobing shown in Nelumbo and Nymphaea.

There is a structure present in various Helobiae which deserves special attention in discussions on the relationship of the Nymphaeaceae. The so-called macropodous embryos of Halophila, Ruppia, Zostera and other genera appear to the writer to throw considerable light on the peculiar structure of the Nymphaea embryo. The enormous development of the basal or hypocotyledonary region of the embryo in such widely separated genera shows a strong and peculiar tendency in the group of Helobiae. In such typical forms as Sagittaria latifolia, Zannichellia palustris

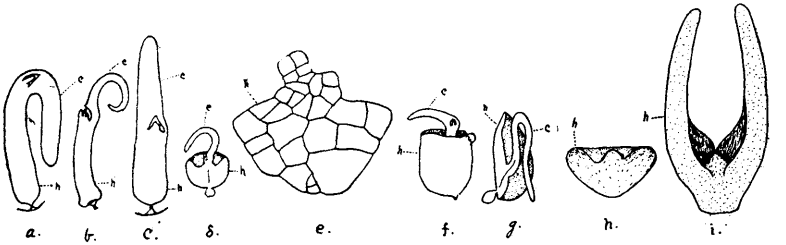


Fig. 1. Similar parts are indicated as follows: c, cotyledon, and h, the basal or lateral region developed into an expanded organ in some embryos. a—Embryo of Sagittaria latifolia. b—Embryo of Zannichellia palustris. c—Embryo of Vallisneria spiralis. d - Longitudinal half of embryo of Halophilia ovalis, after Balfour. e—Section of young embryo of Erythronium americanum showing beginning of massive development of basal region. f—Embryo of Ruppia rostellata, after Wille. g—Longitudinal half of embryo of Zostera maritima, after Rosenberg. h—Young embryo of Nelumbo lutea, after Lyon. i—Older embryo of Nelumbo lutea, after Lyon.

and Vallisneria spiralis (Text Fig. 1, a, b, c) there is barely a hint of such a development. In some other Monocotyls, as, for instance, in Erythronium americanum, the basal region of the embryo early shows a rapid development, growing into a massive, lobed structure which functions as an absorbing organ (Text Fig. 1, e), This is no doubt the purpose of the massive expansions and lobes present in Halophila, Ruppia, Zostera, Nelumbo, Nymphaea and Castalia (Text Fig. 1, d, f, g, h, i, and Figs. 14–19). To the writer there is no more reason for calling the ridge or lobes of the Nymphaeaceae, cotyledons, than the remarkable expansion at the base of the embryo of Zostera. The basal expansion in the Castalia embryo, to the writer, cannot represent the same or homologous structure as the cotyledons of Sagittaria or Bursa. According to this view the so-called cotyledons of Nelumbo, Nymphaea and Castalia represent hypocotyledonary

expansions homologous to the expansions found in Zostera and other genera of the Helobiae.

It appears to the writer that the supposition that all so-called cotyledons are homologous is probably erroneous. The type of embryo found in Sagittaria and Alisma is in fact rather exceptional among Monocotyls and must be regarded as ideal rather than typical of the class. Neither is the fact that the plumule develops as a terminal structure to be regarded as at all conclusive for it is said that the plumules in Dioscoreaceae and Commelinaceae are apical. There are also a number of fundamentally different types of Dicotyl embryos. Instead of having two general types in Angiosperms there are several types, and these approach each other at various points in widely separated orders. The division line between Monocotyls and Dicotyls is, after all, not

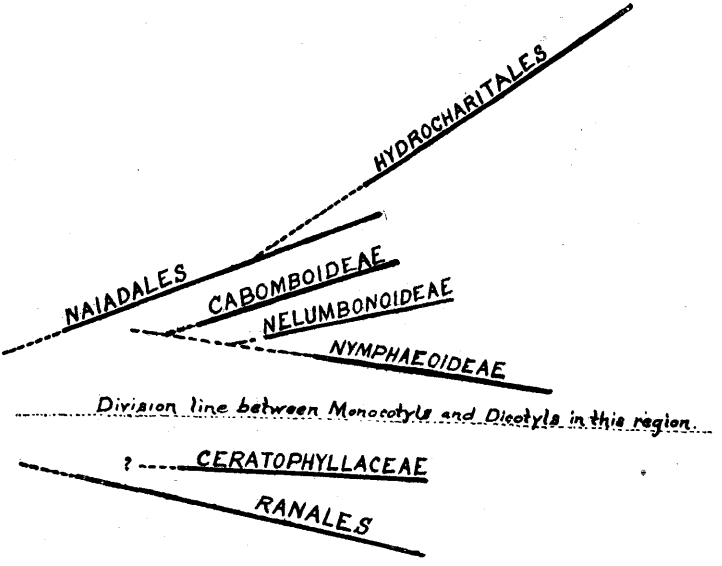


Fig. 2. Diagram of relationship between Helobiae, Nymphaeaceae and Ranales.

very distinct. Although Angiosperms are far removed from all other plants, they represent such a vigorous modern group that there has not been time for the extinction of intermediate forms. With the removal of a few connecting groups it would be more easy to recognize six or seven classes of Angiosperms instead of two.

With our increasing knowledge of the embryogeny of Angiosperms it is becoming more and more apparent that the mere difference in the character of the embryo is not sufficient to determine the position of a genus or family. All possible characters

during the life cycle must be taken into account, otherwise the result will be largely artificial. As intimated above, the writer, through paleontological studies, came to the conclusion a number of years ago that Monocotyls did not come from Dicotyls nor Dicotyls from Monocotyls; that the Angiosperms do not represent two sharply defined classes, but that there are a number of lines of development from some common stock; and that on this account there are frequent independent duplications of important characters in quite distinct series of forms. According to the views expressed above the relationship of the groups under discussion may be represented as shown in the diagram (Text Fig. 2).

Since lists of the important literature have recently been given in a number of papers, it is not necessary to add an extensive bibliography here.

1. LYON, H. L. Observations on the Embryogeny of Nelumbo. Minn. Bot. Studies **2**: 643–655. 1891.
2. COOK, M. T. Development of the Embryo-sac and Embryo of Castalia odorata and Nymphaea advena. Bull. Torr. Bot. Club **24**: 211–220. 1902.
3. CONRAD, H. S. Note on the Embryo of Nymphaea. Science **15**: 316. 1902.
4. CAMPBELL, D. H. On the Affinities of Certain Anomalous Dicotyledones. Amer. Nat. **36**: 7–12. 1902.

EXPLANATION OF PLATES V–VII.

The diagrams represent typical flowers selected from a series of variable types and show the actual number and position of the floral organs. The other figures were drawn with the aid of an Abbe camera.

PLATE V.

Fig. 1. Section of vascular bundle from the peduncle of Nelumbo lutea.
Fig. 2. Diagram of flower of Alisma plantago.
Fig. 3. Diagram of carpellate flower of Sagittaria rigida.
Fig. 4. Diagram of staminate flower of Sagittaria rigida.
Fig. 5. Diagram of carpellate flower of Sagittaria latifolia.
Fig. 6. Diagram of staminate flower of Sagittaria latifolia.

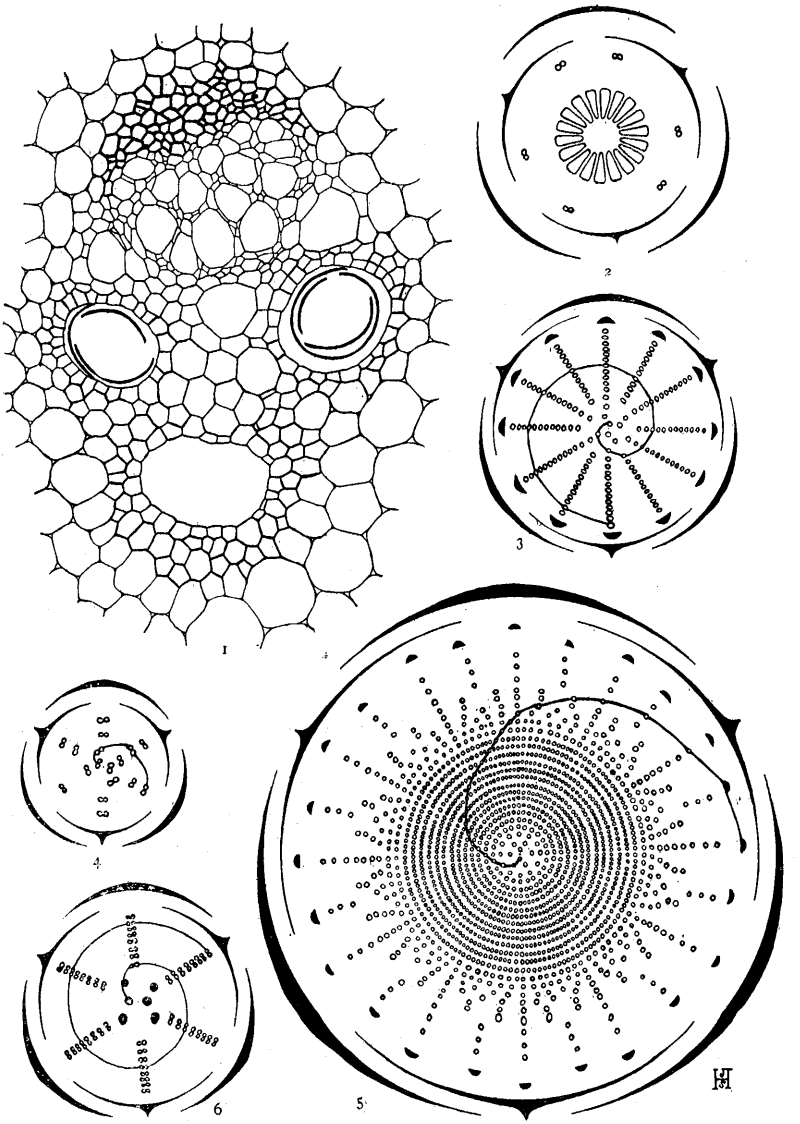
PLATE VI.

Fig. 7. Diagram of flower of Cabomba caroliniana.
Fig. 8. Diagram of flower of Brasenia purpurea.
Fig. 9. Diagram of flower of Potamogeton natans.
Fig. 10. Diagram of flower of Nymphaea advena.
Fig. 11. Diagram of flower of Castalia odorata.
Fig. 12. Diagram of flower of Castalia tuberosa.
Fig. 13. Diagram of flower of Nelumbo lutea.

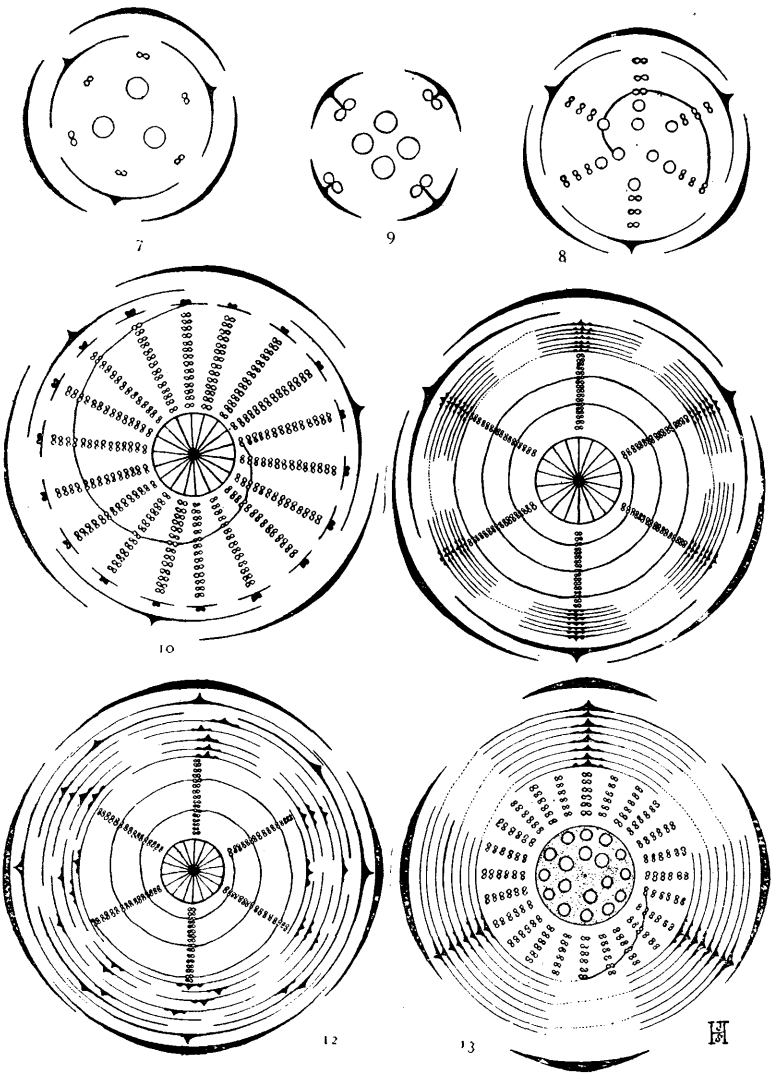
PLATE VII.

Fig. 14. Young embryo of Nymphaea advena.
Fig. 15. The same embryo as in Fig. 14, back view.
Fig. 16. Young embryo of Castalia odorata.
Fig. 17. Older embryo of Castalia odorata, upper side.
Fig. 18. The same embryo as in Fig. 17, under side.
Fig. 19. Still further developed embryo of Castalia odorata, showing "Dicotyl" appearance.

OHIO NATURALIST. *Plate V.*



SCHEFFNER on "Nymphaeacae and Helobiae."



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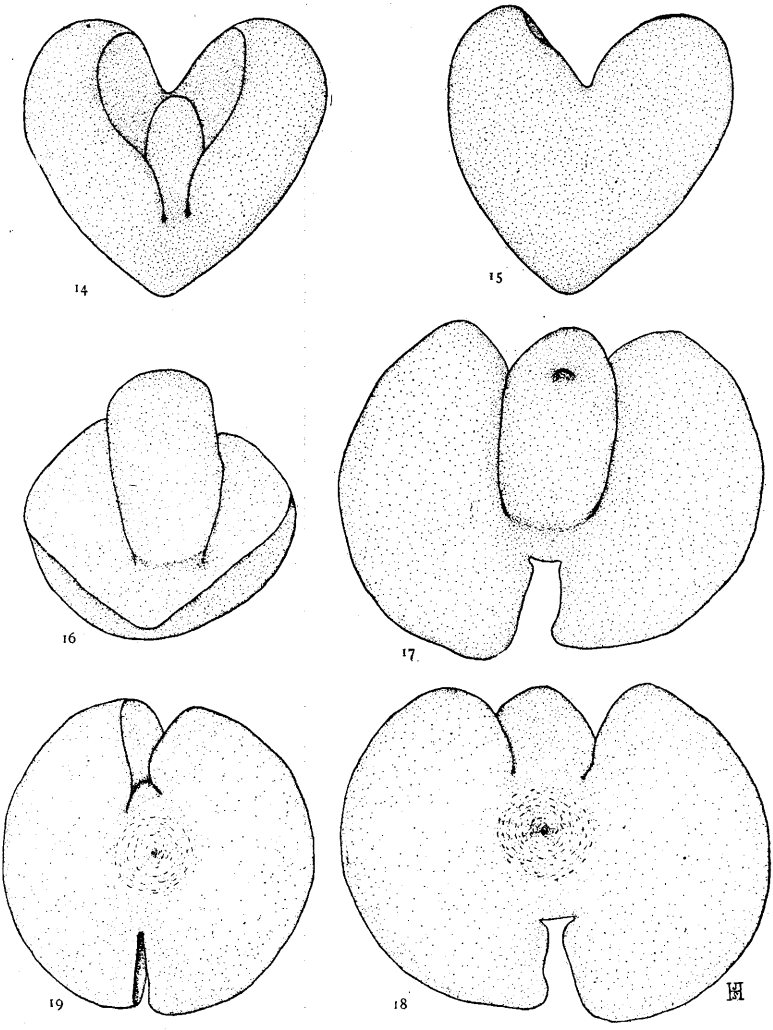
OHIO NATURALIST. *Plate VII.*



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